A CONTRIBUTION OF RAIN FOREST RESEARCH
TO EVOLUTIONARY THEORY[1,2]

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Though by no means universal even in the lowlands, species diversity within a single life-form reaches unequalled levels in many tropical forests, and in particular in the aseasonal wet oceanic climates of the Far East. There large genera, many of whose species may occur together and are apparently spatially interchangeable (e.g., Poore, 1968) are particularly frequent and have prompted speculation as to their origin. Ecologists (Poore) and taxonomists (Fedorov, 1966; van Steenis, 1969) alike have concluded that chance events are the major determinants of survival and must hence influence the course of evolution. Janzen's (1970) attractive theory that interactions between host-specific predators and their tree prey provide a density controlling mechanism which allows accretion of floristic diversity has yet to be investigated within large tree genera and does not apply within the Dipterocarpaceae, dominant trees of the Far Eastern rain forest canopy, whose predators are well known and are not specific even at generic level.

How old are tropical tree species? How niche specific are they? Is evolution continuing within these forests? Are these communities in evolutionary equilibrium, following a long period of gradual stabilization (e.g., Stebbins 1974), or does species diversity continue to increase? What are the component tree species, are they outbreeders and are they genetically variable, or are they genetically uniform, even apomictic?

Richards (1963) has reasoned that ecology cannot afford to ignore the tropics; an understanding of the evolutionary biology of this most species-rich vegetation must be accepted as equally essential if only to put, by comparison, knowledge of our younger and less diversified temperate counterparts into truer perspective. Studies in the Dipterocarpaceae and their forests over the last 20 years, in which I have collaborated, are beginning to elucidate this subject.

THE AGE OF WEST MALESIAN FOREST ECOSYSTEMS

Haile et al. (1977) have established that the Malay Peninsula and southwest Borneo have remained within 20° N. latitude of the equator since the late Cre-

taceous. Muller (1968, 1972) has described the transition from gymnosperm forest to predominantly angiosperm forest during and following the Cenomanian, and the successive accretion of new orders and families through the Tertiary, from pollen analysis of the Plateau Sandstone formation of northwest Borneo. By the end of the Tertiary the inland forest flora was apparently not dissimilar to that of the present day, fossil leaves of putative Pliocene age from Manila for instance (Merrill, 1923) being identifiable with species still growing nearby. The pollen record suggests, on the one hand, that the region has remained within the humid, though not necessarily aseasonal, tropics since the origin of angiosperm forest, and, on the other, that the growth of floristic diversity at ordinal and familial level has occurred through a sequence of periodic and rather sudden immigrations, rather than through gradual evolution in situ.

The Quaternary era must inevitably have witnessed the invasion of seasonal rainfall regimes during the periods of eustatic fall in sea level, when the Sunda Shelf region, comprising the Malay Peninsula, Sumatra, Java, Borneo and the intervening seas, became a continent comparable in size and latitude to the northern part of South America; the last such time ended ca. 15,000 years B.P. The only evidence for climatic change in the lowlands during the Pleistocene is indirect, through the existence and gradual extinction of the nonforest large mammal and essentially Asiatic Trinil fauna during mid-Pleistocene times in Java (Medway, 1972). Evidence for the existence of periods of rainfall seasonality from other parts of lowland Sundaland during the Pleistocene is presently lacking. It is nevertheless difficult to believe that the extraordinary species richness of west Malesian forests, which is strongly restricted to the aseasonal region south of the Kangar-Pattani line in the Peninsula (Whitmore, 1975)—though generic diversity is not restricted to the same extent—has arisen in the last 15,000 years; the exceptionally high level of local endemism in some coastal regions, notably east and northwest Malaya and along the northwest coast of Borneo, almost certainly has a more ancient origin. Indeed, whereas localized centers of diversity and endemism exist in a sea of uniformity in South American forest ecosystems, and are considered to indicate the sites of refugia for rain forest species during the interpluvials, the greater part of the present west Malesian archipelago must be regarded as analogous to one vast refugium fragmented by the current high sea level.

RATE OF SPECIATION WITHIN WEST MALESIAN TREES

Muller (1964, 1972) has identified the pollen type of the monotypic riparian palm *Nypa* from as early as the Upper Cretaceous, and in another unique palynological study traced evolution within the mangrove genus *Sonneratia* and its fossil progenitor *Florschuetzia* since the Eocene. Plant distributions provide indirect evidence for continuing speciation during the Pleistocene and up to the present day; in this respect dipterocarps are particularly apt subjects owing to the absence of any known fruit vector. This may be exemplified by comparing distributional patterns in Dipterocarpaceae with the postulated Pleistocene geomorphological history of the northwest Borneo neogeosyncline (Ashton, 1972; Wall, 1967); the history of river capture neverthless remains to be confirmed by

108 are widespread, but:-

57 are confined E. or W. of the ancient river Lupar, whose course during Pleistocene periods of continentality is marked by submarine canyons northwards towards the continental shelf.

Only 7 are confined by the Rejang, largest river in northern Borneo; its present course seems to have resulted from late Pleistocene river capture.

27 are confined by the insignificant Kemena, which nevertheless follows the putative former Rejang valley.

3 species are confined E. or W. of the Suai-Sibuti drainage, which follow the putative Pleistocene valley of the Baram, a major river which limits no species range.
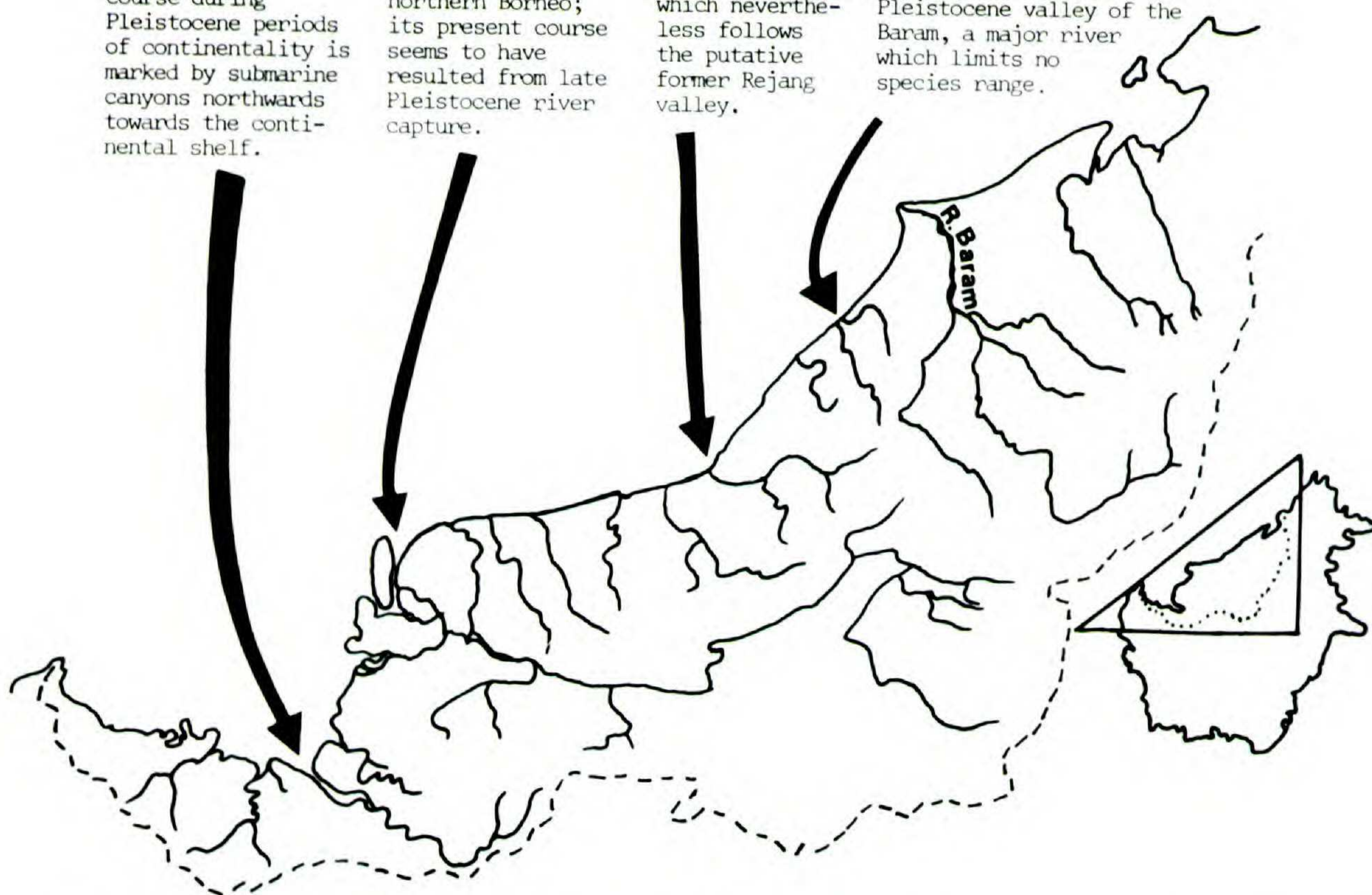
FIGURE 1. Geographical barriers and the distribution of 201 dipterocarps in northwest Borneo. The southeast to northwest trending drainage of northern Borneo is of probably late Pliocene-early Pleistocene origin.

analysis of river sediments. Though the major discontinuity in dipterocarp distributions follows a river valley of probably pre-Pleistocene origin, significant discontinuities also occur across valleys of lesser age, including examples of allopatric subspeciation (Figs. 1–2).

In some cases species may be remarkably recent in origin: The ten species of *Shorea* sect. *Pachycarpae* are endemic to Borneo, surprising in itself in view of its intermittent connection with the rest of Sundaland until the Holocene. Of these only one, *S. mecistopteryx* Ridl. is invariably morphologically clearly defined and at the same time widespread. The other widespread species, *S. pinanga* Scheff., *S. amplexicaulis* Ashton, *S. beccariana* Burck, and *S. macrophylla* (de Vr.) Ashton, are very variable and morphologically intermediate forms occur frequently in certain restricted localities. Of the remainder, at least two, *S. praestans* Ashton and *S. rotundifolia* Ashton, seem by their extremely local distribution, as well as by their morphological relationships with others, to be of very recent origin; the latter for instance occurs sympatrically, even side by side, with *S. amplexicaulis* with which it appears to be closely related.

CAUSES OF SPECIATION: AN ECOLOGICAL VIEWPOINT

Nevertheless, *S. rotundifolia* and the species in its section are exceptional among dipterocarps: Most species of the humid tropics are clearly defined;
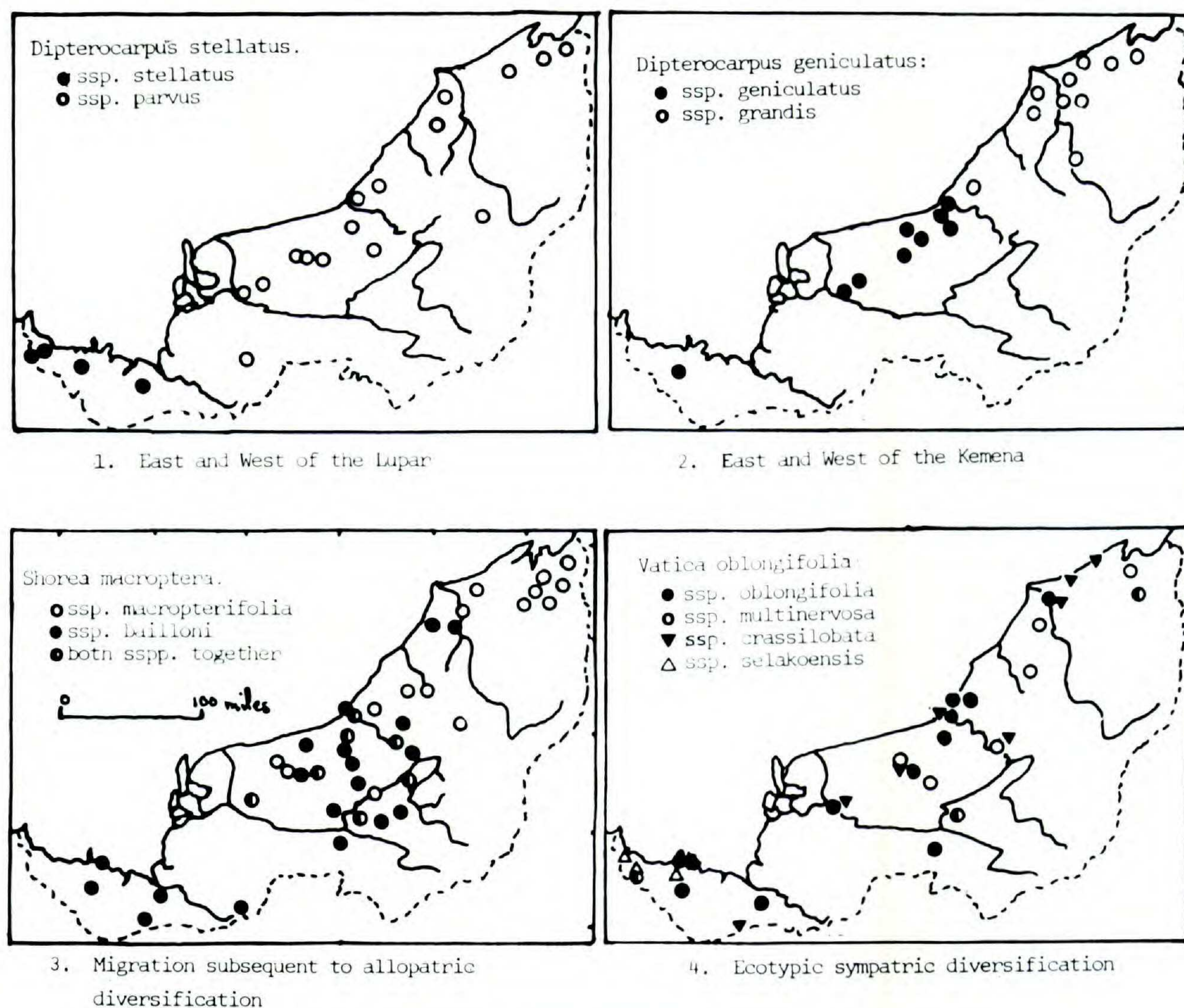
FIGURE 2. Patterns of speciation in dipterocarps in northwest Borneo.

closely related taxa are as a rule ecotypically differentiated in relation to site (Ashton, 1964, 1969), habit (Ashton, 1969), or physiology, as is the case with the commoner sympatric species of *Shorea* sect. *Muticae* (Symington, 1943). It is at the generic and familial level that taxa appear to be ecologically complementary, and it may be at this level that the importance of predator-prey interactions play a major part in the maintenance of diversity. This is yet to be studied, but it would be surprising if successful speciation occurred among rain forest trees in response to predators whose life cycle is likely to be at least one hundred times shorter.

Figure 3 shows that it is the extraordinary diversity at species level which distinguishes Malesian forests from all others. The sample from mixed forests in Surinam (calculated from Schulz, 1960, and probably a slight underestimate as species in some genera were not all distinguished) produced the same genus to species ratio as that from the isolated relict forests of southwest Sri Lanka, notwithstanding the higher number of genera in the former, a reflection of its continental location. Pasoh forest has one of the lowest ratios calculated for Malesian Mixed Dipterocarp forest (e.g., see Ashton, 1976a).

Mixed Dipterocarp forest differs considerably between sites, both in species
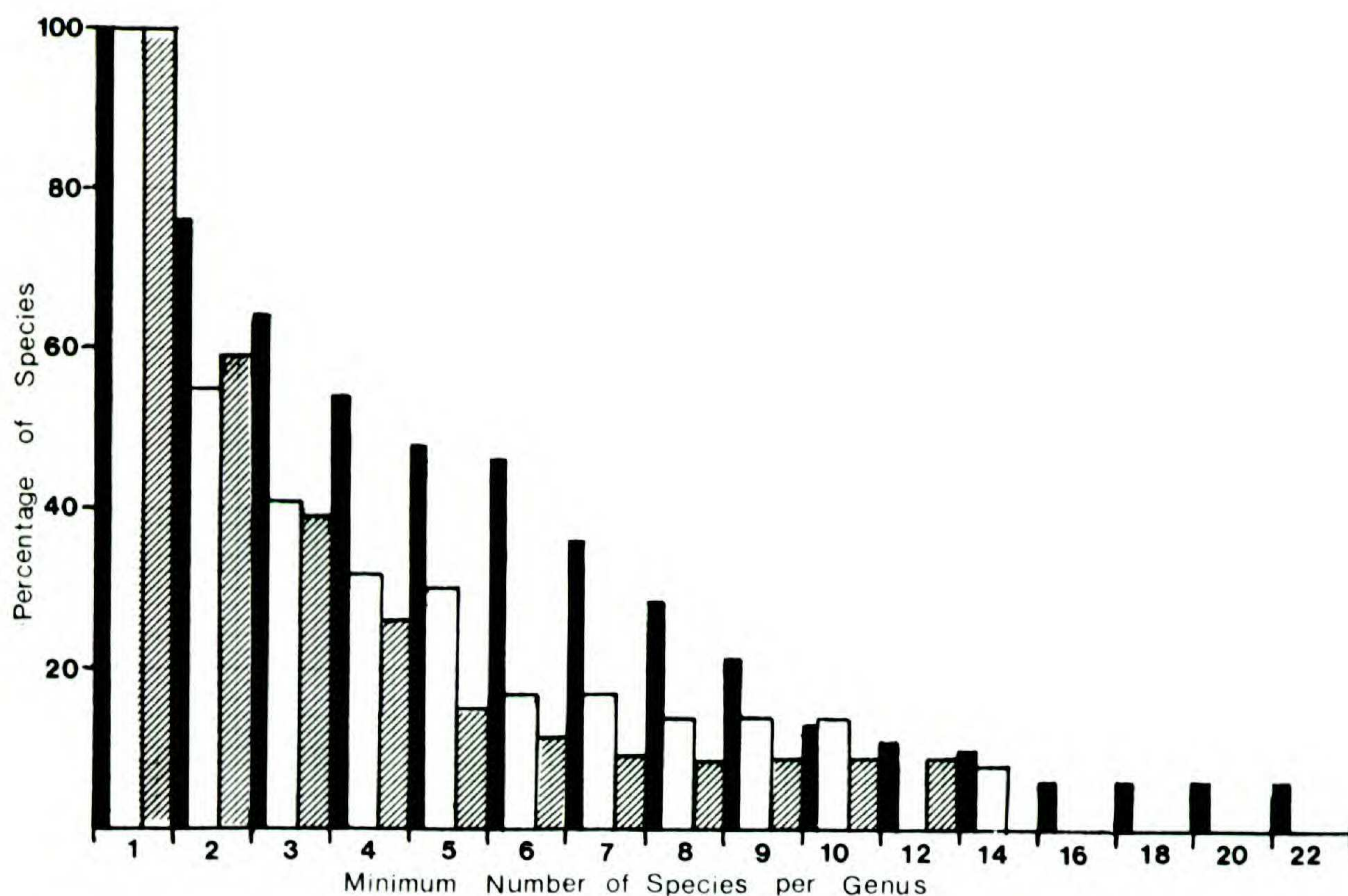
FIGURE 3. The percentage of species in genera of different sizes in samples of uniform mixed lowland rain forest. Solid columns: Pasoh Forest, Malaysia (2 × 5 ha; 191 genera; 484 species; ratio 1 : 2.5). Empty columns: Sri Lanka (3 × 2.5 ha; 98 genera; 166 species; ratio 1 : 1.7). Hatched columns: Mapane, Surinam (5.6 ha; 152 genera; 255 species; ratio 1 : 1.7) .

richness and in degree of floristic spatial variability; and both seem to be influenced by soil nutrient status. Our work in northwest Borneo indicates that spatial variation is measurably correlated with soil nutrients only where fertility is low; total phosphorus and exchangeable potassium become increasingly correlated when phosphorus levels are below ca. 200 p.p.m. (Fig. 4; Ashton & Brunig, 1975; Ashton, in preparation). Intrinsic floristic richness appears to be greatest where exchangeable potassium is between 1,000–2,500 p.p.m. (Fig. 5). Here a species/individual curve for a Heath forest site is compared with six others, selected to exemplify a general trend among 18 sites in Malaysian Mixed Dipterocarp forest where I have carried out quantitative studies. The Pasoh curve is representative of the Mixed Dipterocarp forest of the Malay Peninsula, noted for its floristic uniformity (Wong & Whitmore, 1970, though see also Ashton, 1976c), growing in a region of Lower Palaeozoic rocks that are the oldest in west Malesia, and on an ancient land surface that has remained above sea at least since the Cretaceous. The plot was sited on Pleistocene raised riverain alluvium to ensure uniformity; forest on adjacent hillside in the event produced a very similar species/area curve. The Arip and Mersing sites each represent small islands, in neither case exceeding 50 km², of an unusual substrate in the sedimentary rocks of the geologically and geomorphologically young Neogene basin of northwest Borneo; the former in fact consists merely of a narrow ridge, rarely exceeding 1.6 km wide. Bukit Lambir, near the youngest part of that basin, is Upper Miocene sandstone. These curves suggest then that intrinsic floristic di-
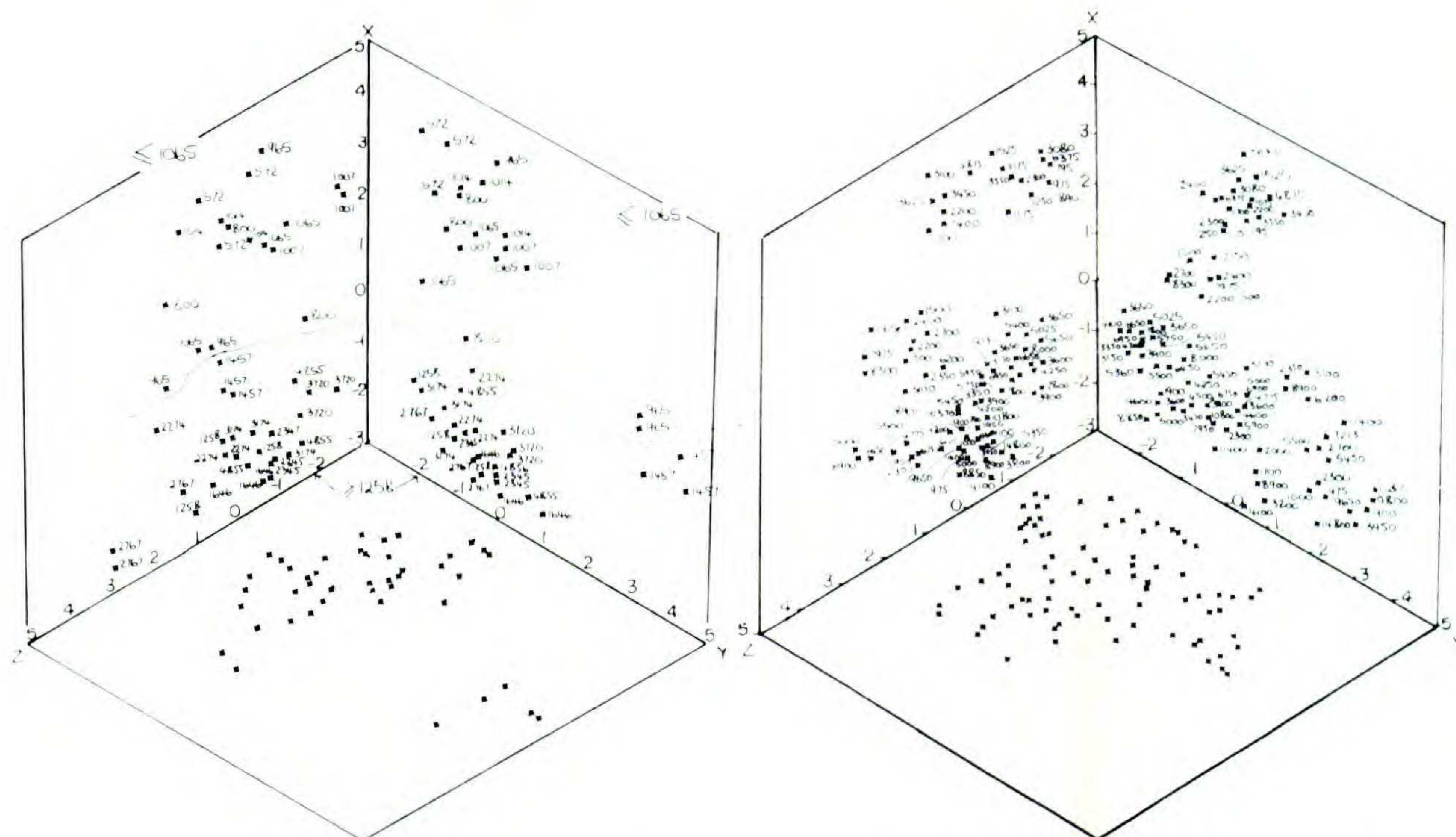
FIGURE 4. Principal components ordinations of 0.2 ha plots in Mixed Dipterocarp forest: Values for exchangeable K (in p.p.m.) are superimposed. Left: Bukit Iju, Arip (rhyolite). Right: Bukit Mersing, Arap (basalt).

versity within this region of probable Pleistocene climatic continuity is a function neither of geological or geomorphological age, nor of the area of uniform terrain and its potential influence on diversification and extinction. They do suggest that an equilibrium may be reached, in which either no further speciation is occurring, or immigration and speciation are being balanced by extinction; and that in the absence of disturbance the level of this equilibrium is determined by soil conditions.

GENETIC VARIATION IN SPECIES POPULATIONS AND ITS MAINTENANCE

It is as a consequence of these discoveries that a group of collaborators in the University of Malaya and the University of Aberdeen, including both staff and research students, has been investigating the genetic variability of tree populations in the mature phase of primary rain forest in Malaya, and the underlying characteristics of cytology, embryology, and reproductive biology, including the behavioral ecology of pollen and fruit vectors, associated with it. This research, centered at the Pasoh Forest, is presently in progress and mention will therefore only be made to results already submitted for publication.

The two principal species under study are Shorea (sect. *Muticae*) *leprosula* Miq., a common, widespread and morphologically well defined and rather uniform emergent dipterocarp, and *Xerospermum intermedium* Radlk., Sapindaceae, an understory fruit tree with similar distribution and variability. Electrophoretic analysis of isozymal variation of populations of both species, coupled with biometric analysis of morphological variation by Y. Y. Gan (Gan et al., 1977) suggest that both have high levels of genetic polymorphism, but that vari-
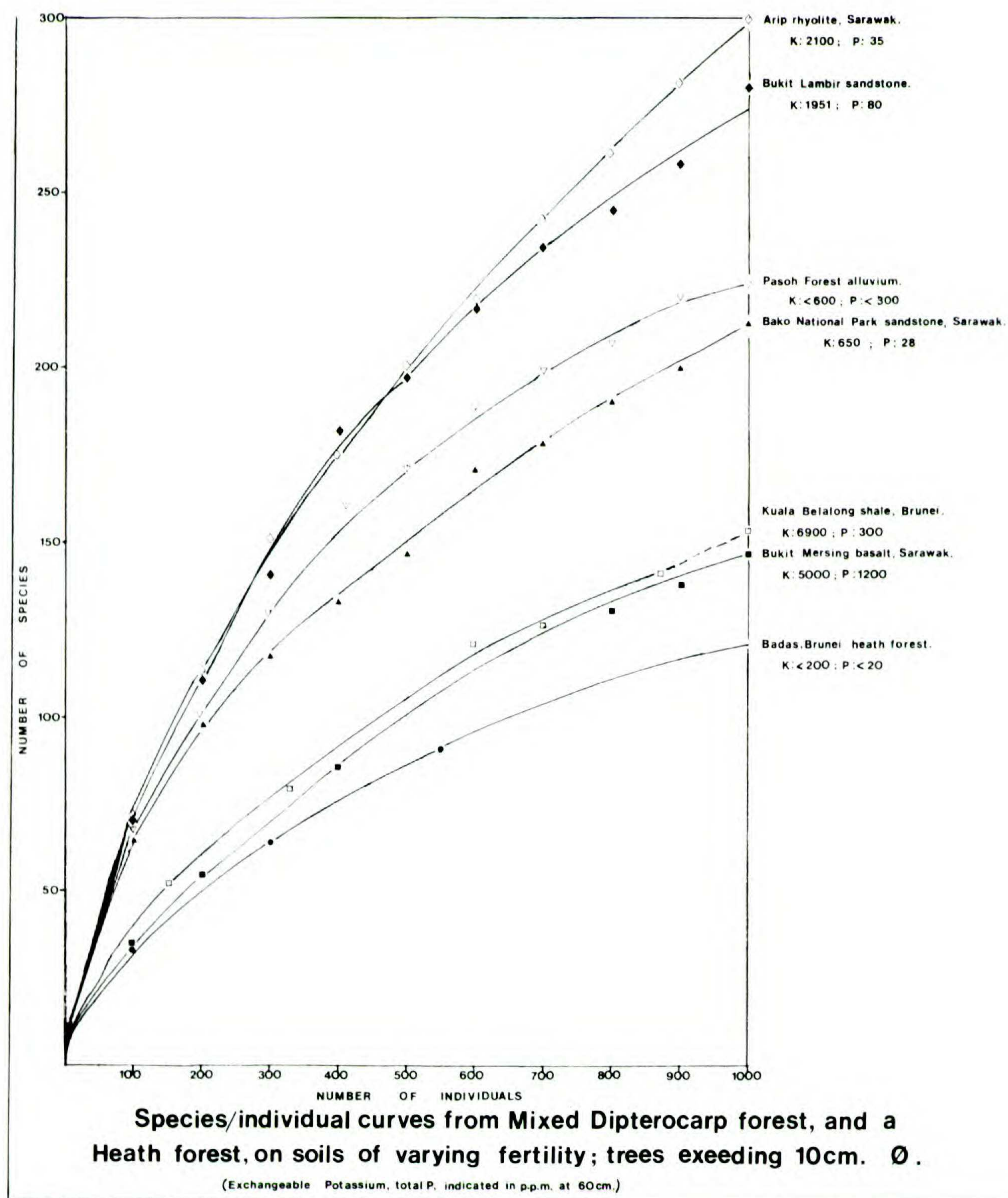
FIGURE 5. Species/individual curves from Mixed Dipterocarp forests and a Heath forest.

ation in gene frequency is short range. It is inferred from this that they are out-breeders with restricted pollen and fruit dispersal; this is being confirmed by studies of pollen compatibility and reproductive and vector biology (S. K. Yap, H. T. Chan & S. Appanah, in preparation). A. Kaur and C. O. Ha (Kaur et al., 1978) find both species to be diploid, with normal embryogenesis of the *Polygonum* type. Chan has also confirmed high levels of self-incompatibility in two species of *Shorea* sect. *Pachycarpae* and successfully secured fruit formation from an artificial hybridization between them.

These species therefore conform to the pattern expected of long-lived plants in stable environments (e.g., Stebbins, 1958) and to the prevailing trends observed by Bawa (1974, 1975, 1977) in similar studies in Costa Rica.

Nevertheless, *Shorea leprosula* and *Xerospermum intermedium* were chosen for study for practical reasons, owing to their relatively high population densities at Pasoh: 5 per ha exceeding 10 cm diameter for the former, 10 per ha for the latter, the mean for all species being 1 per ha. Species with low population densities comprise the vast majority, and it might be expected that maintenance of free gene exchange may be more difficult among them. Gan et al. (1977) found a very low level of genetic polymorphism by isozyme analysis in *Shorea ovalis* (Korth.) Bl. ssp. *sericea* (Dyer) Ashton, a result which may nevertheless be an artifact caused by the fact that this species is a tetraploid (Jong & Lethbridge, 1967). Jong (1976) reported meiotic irregularities in the same species. Chan (in Gan et al., 1977; Kaur et al., 1978) found that *S. ovalis* appears to be fully self-compatible, and, though lacking the close intraspecific flowering synchrony that is a characteristic of most dipterocarps, it has a more uniform than average fruiting success rate. A. Kaur (Kaur et al., 1978) has now confirmed that apomixis occurs in this species and at least one other through adventive polyembryony. Apomixis is also inferred through the constant occurrence of triploidy in root squashes from several seedlings originating from a single tree, and from the production of more seedlings from a fruit than there are ovules in several others. Among 16 dipterocarp species studied quantitatively by us, 10 at least sometimes produced multiple seedlings from the normally 1-seeded fruit, though this does not confirm polyembryony as the dipterocarp ovary initially bears 6 ovules. In the four species in which several individuals were under observation the proportion of seeds producing multiple seedlings varied widely between individuals. Though it is unlikely that apomixis occurs through adventive polyembryony in all species producing multiple seedlings, it equally cannot be assumed that it does not occur in species in which only single embryos develop.

C. O. Ha (in Kaur et al., 1978) has inferred apomixis in the dioecious understory tree *Garcinia parvifolia* Miq., and has inferential evidence for its occurrence in other species of *Garcinia*. If we accept Grant's (1958) view that dioecism is itself a derived condition, then apomixis must here be regarded as evidence of extreme derivation, and an example of the advanced evolutionary levels that can occur, presumably as a result of natural selection, in the rain forest environment.

Though it can hardly be claimed that these few species can adequately represent the West Malesian lowland tree flora as a whole, they do conclusively demonstrate that apomixis occurs within those series of closely allied species, occurring together in the same habitat, which are such a unique character of that region.

An unexpected observation is that those species whose genecology might be expected to favor allopatric diversification and distinct discontinuities in variation, *Shorea leprosula* and *Xerospermum intermedium*, are remarkably uniform throughout their wide range, while every one of the dipterocarp taxa in which

apomixis is inferred or confirmed are morphologically distinct and possess closely allopatric distribution patterns. Some, such as *Shorea ovalis*, occur in relatively high density populations and are widespread, while others such as *Hopea subalata* Sym. are extremely local; this will form the subject of a forthcoming paper.

TOWARDS A SYNTHESIS

To help identify priorities for future work we suggest the following hypothesis to explain our observations: In the uniform physical environment and predictable climate of lowland Malaya natural selection will be dominated by biotic factors. These factors will continuously change in time through the periodic accretion of immigrant species into the forest community, each newcomer thus inevitably modifying the competitive interactions of those already present. The maintenance of genetic variability within species is therefore essential to their long-term survival, and maintenance of cross-pollination is at a premium. As the density of the forest community as a whole cannot increase, it must follow that the arrival of new species, and particularly those which successfully build up relatively high population densities must lead to a compensatory decline in the population density of those already present. This will hasten the decline of species whose densities are already low by increasing the physical difficulty of cross-pollination from increasingly distant pollen sources as Fedorov predicted; this in turn will lower fruit yield and weaken the reproductive pressure required for maintenance of numbers. Natural selection in species with very low population densities—and these could constitute the majority—might well favor genotypes that are both well adapted and can maintain reliable and high fruit production. It is suggested therefore that apomixis has originated in rain forest trees once again as a means of overcoming sterility, as suggested long ago by Darlington (1939).

We might infer, from the variability between trees in the proportion of multiple seedlings produced, that apomixis occurs in only a proportion of trees in some species populations. It is difficult nevertheless to see how a balance between the number of apomictic and/or self-compatible, and obligate outcrossing individuals can be maintained in perpetuity, for increasing rarity due to changing interspecific competition would lead to increasing decline in the proportion of obligate outcrossing individuals. Conversely obligate apomixis, or gene fixation in small isolated populations of self-compatible individuals, must itself be regarded as an evolutionary dead end, preluding inevitable extinction in a continuously changing biotic environment. Thus the maintenance of low levels of self-compatibility, and sufficiently high population densities to ensure adequate reproductive pressure to maintain numbers through outcrossing are both essential adjuncts to long-term survival of a species. If obligate apomixis does frequently occur (and this requires much more study) and if our hypothesis is correct, we may see in the ancient Malayan rain forest a phenomenon which must eventually arise in all plant communities: there must be an ultimate limit to the level of intrinsic species diversity that can be attained, beyond which accretion is balanced by extinction (see also discussion in Whitmore, 1975).

We have here an analogue of G. G. Simpson's (1953) "evolutionary episode"

in the context of a multispecies community. Invading species, we suggest, are mainly outbreeders, but the low densities of even the commonest species combine with limited pollen and fruit dispersal to favor rapid allopatric speciation; such species will prevail in young forest communities and this can be tested in the isolated forests of volcanic islands or the Atlantic foothills of the Central American Cordillera. When numbers decline through competition, and as the overall floristic diversity increases, selection will increasingly favor apomixis which may then be an agent of secondary, essentially ephemeral and possibly sympatric, speciation. Thus the declining species do not fade away gradually but, by borrowing time in a Faustian pact of apomixis, regain the stage from time to time before their inevitable nemesis.

CONCLUSIONS

We now have growing evidence then that Malesian trees of the mature phase of primary rain forest are highly niche specific; that some may be old, but that speciation is actively continuing among many others; that there is a maximum number of species that a forest can accommodate, that this varies with site conditions and that it has already been approached in west Malesian forests; and that a remarkable variety of breeding systems exists even within the mature phase alone. An overall picture is thus beginning to emerge in which each part of the puzzle is becoming interlocked, but it hardly confirms Stebbins's (1974) picture of the tropical rain forest as merely a repository for botanical antiques!

But what of the gap phase species—the woody pioneers? How have so many archaic forms continued to survive nevertheless? And what are the mechanisms that allow species diversity to reach its highest level on relatively infertile soils? A student of ours is about to embark on a study of the first, and we are planning to pursue the others in the near future. But our forest of ignorance is deep and vast, and for all its intriguing mystery attracts far too few explorers.

Once again the fascination of academic theory has dominated my presentation, but what are the realities on the ground? Raven (1976) has eloquently described the demise of this unique vegetation; man's destruction in pursuit of short-term gains will lead to long-term disaster for humanity, as inevitably as apomixis may for my proud dipterocarps. Everywhere it is the same—uncontrolled and injudicious logging practices and immigration of peoples unfamiliar with local agricultural conditions, leading to destruction of the hydrological balance of catchments, physical erosion, flooding and silting of the fertile plains, the supremacy of perennial herbaceous weeds, and the final destruction of social systems and starvation. We biologists have for too long pointed our accusing fingers elsewhere, at the politicians, financiers, even the poor peasants, anyone but ourselves. I would suggest that two of the most intractable problems are essentially scientific: The lack of critical research into the most effective means of bringing about progressive change in land use based both on scientific innovation and traditional practices and values; and the tendency for us scientists to go for the easy options—be it the investigation of an isolated academic problem or the development of a technique to enhance short-term profitability without regard to its wider implications—and to fear the interdisciplinary collaboration

on a broad front that alone can provide the prescriptions needed. Our little venture may claim to be a hesitant start in the right direction (Jong et al., 1973; Ashton 1976a, 1976b), for in it we combine research education with a conscious choice of species which have potential in plantations, for timber and fruit. Now we must use the knowledge we have gained to experiment in the establishment and improvement of new crops for new lands—those that were considered unexploitable by traditional farmers and are now all that is left. We must get these crops from the much-heralded gene pool of the forest, and this we plan too. But we will need economists, agronomists, social anthropologists, and others besides before our work can reach the stage of practical applicability. Above all, we need collaboration.

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